

BEHAVIORAL ECOLOGY OF THE "EDGE EFFECT"
IN *SCHIZOCOSA CRASSIPES* (ARANEAE: LYCOSIDAE)¹

BY WAYNE P. ASPEY²

Department of Zoology and Microbiology
Ohio University, Athens, Ohio 45701

INTRODUCTION

The "edge effect" is the phenomenon of increased variety and density of organisms at ecotones (i.e., transitions between two or more diverse communities, such as between forest and grasslands), and is well-known in birds (Beecher, 1942; Johnson and Odum, 1956) as well as in insects and spiders (Luczak, 1966; Luczak and Dabrowska-Prot, 1966; Dabrowska-Prot and Luczak, 1968; Luczak, 1968; Edgar, 1971; Dr. R. Blanke, personal communication). Such community junctions are narrower than the adjoining communities, although they may have considerable linear extent. Additionally, ecotones contain organisms from each of the overlapping communities, as well as the "edge" species, those organisms restricted to, or spending most of their time in, the transition zone (Odum, 1959).

While studying the behavioral biology (Aspey, 1974, 1975, 1976a,b) and environmental physiology (Aspey, Lent, and Meeker, 1972) of several wolf spider (lycosid) species, I found abundant numbers of these spiders in restricted areas at the forest-meadow interface. From a practical point of view, the ability to predict locations of large spider populations facilitated collection for laboratory studies. However, identifying those aspects of the environment or of the spider's behavioral biology that determine

¹This study was supported in part while the author was a Hiram Roy Wilson Research Fellow in Zoology at Ohio University, and published with the aid of The Marine Biomedical Institute, The University of Texas Medical Branch at Galveston, Texas.

²Present address: Division of Comparative Neurobiology & Behavior, The Marine Biomedical Institute, The University of Texas Medical Branch, 200 University Boulevard, Galveston, Texas 77550.

Manuscript received by the editor March 4, 1976.

the edge effect poses interesting considerations. For example, possible ecological and behavioral variables include: (1) availability of food organisms; (2) weather parameters such as temperature and humidity; and (3) social behavior and organization of the animals. With regard to food availability, Luczak and her colleagues (Dabrowska-Prot, Luczak, and Tarwid, 1966; Luczak, 1966; Luczak and Dabrowska-Prot, 1966; Dabrowska-Prot and Luczak, 1968) observed high densities of lycosids at the forest-meadow interface and attributed such spider concentrations to the presence of large prey (i.e., mosquito) populations.

With regard to environmental parameters, Nørgaard (1951) demonstrated that microclimate is an important factor in separating two related lycosid species having different habitat and environmental tolerances. Using mark and recapture techniques in the field, Kuenzler (1958) found evidence of individual home ranges in *Lycosa* spp., and activity levels within these limited areas were positively correlated with temperature and humidity. Hallander (1967) considered courtship in relation to habitat selection in *Pardosa chelata*, and found temperature thresholds to be important for courtship display to occur. Finally, in a comprehensive study on habitat selection and distribution of 15 wolf spider species on coastal sand dunes, Almquist (1973) found daily or seasonal changes in weather often resulting in migration. Almquist (1973) concluded that habitat selection was fundamentally controlled by those microclimatic and vegetational conditions satisfying the spiders' temperature and humidity requirements. Thus, while lycosids exhibit certain physiological tolerances to extremes of environmental conditions (Aspey et al., 1972), they select their habitat, in part at least, on the basis of microclimate.

With regard to social behavior, Gillette (1968, 1972) has implicated a variety of seemingly non-environmental factors affecting aggregation in the locust, including social determinants in desert locusts (Gillette, 1973). Although eusociality is not known to exist in spiders (Wilson, 1971), there are "social" spiders, as reviewed by Kullmann (1968) and Shear (1970). With the exception of reproductive behavior, little is known about the sociobiology of wolf spiders, and an examination of the social behavior of lycosids may provide additional insight into the edge effect in these animals. To this extent, the present paper examines the frequency of inter-individual encounters among adult *Schizocosa crassipes*

in the natural habitat, and discusses those behavioral and ecological factors which may contribute to making this animal an edge species.

METHODS

Individuals of the brush-legged wolf spider, *Schizocosa crassipes* (Walckenaer), were observed as they interacted in the natural habitat at Stroud's Run State Park, Athens Co., Ohio, USA. Adults of both sexes are approximately the same size (body length = 7-10 mm, carapace width = 3-4 mm, leg span = 27-30 mm), although striking sexual dimorphism exists. For example, the female's variegated, patterned brown coloration contrasts with the male's black coloration and gray/white band down the midline of the cephalothorax and abdomen. Molting to the adult occurs in late May, at which time the males develop conspicuous tufts of black hairs on the tibiae of the forelegs with smaller brushes on the patellae.

These small, ground-dwelling spiders are distributed throughout the eastern United States within the Deciduous Forest Formation, and have been recorded as far West as Nevada (Fitch, 1963). In the present study, *S. crassipes* were found in abundance on leaf litter at the forest-meadow interface in an area approximately 2×15 m, half of which was shaded and half exposed to sunlight.

Observations were conducted continually from 1100-1600 hours every other day for 14 days during May 19-31, 1973, and air temperature was recorded during each observation period. I moved systematically around the study area every 10 min, waiting 5 min after each move before resuming observations. Thirty-five hours in the field resulted in 17.5 hr of recorded observations and totalled 1050 one-minute observation periods. Protocol was recorded on a battery-powered tape-recorder, and included the number and sex of all conspecifics crossing within 1 cm directly in front of a male observation spider every minute. An earlier criterion of any spider approaching another within 3-5 cm, regardless of direction, was discarded because so many spiders were involved that accurate counts could not be taken.

An observation spot was approximately 60 cm in diameter arbitrarily divided into 12 sectors with the perimeter corresponding to the face of a clock. Following each move around the field, data recording began with my position taken as 6 o'clock, and observa-

tions continued clockwise every minute. This procedure, coupled with systematically moving about the field, helped to representatively sample the spider population.

RESULTS AND DISCUSSION

In the natural habitat a given male *S. crassipes* encountered an average of four conspecifics per minute, which included one female and three males (Fig. 1). A Kruskal-Wallis one-way analysis of variance (Siegel, 1956) indicated that air temperature fluctuated significantly during a given observation session, which lasted 6 hours ($H = 14.07$, $df = 5$, $p < .02$, two-tailed). Correspondingly, the greatest number of individuals were encountered at 1300 hours which coincided with the highest mean air temperature (19.4°C). Although the mean number of females encountered by a given male observation spider did not vary with time, the mean number of males encountered varied significantly from 1100 to 1600 hours ($H = 15.75$, $df = 5$, $p < .01$, two-tailed).

This disparity in the sex ratio may be due to: (1) greater numbers of males to females; or (2) greater activity on the part of the males. Field data from nearly 800 *S. crassipes* collected in the same area during 1970-1973 indicated that the male:female ratio was approximately 50:50. It appeared, therefore, that the divergent sex ratio observed during inter-individual encounters reflected motility differences between the sexes. Laboratory analysis of isolated and socially grouped males and females supported this hypothesis in that males exhibited up to 10 times more locomotory activity than females (Aspey, unpublished observations).

Similar motility differences between male and female *Pardosa pullata* and *P. prativaga* have been reported by Richter, den Hollander, and Vlijm (1971), as well as for *Lycosa (Pardosa) lugubris* in the field (Dr. S. W. F. van der Ploeg, personal communication). In *P. amentata*, Vlijm, den Hollander, and Wendelaar Bonga (1970) considered high levels of male locomotory activity as inherent to the male's age and/or related to the egg sac carrying phase of the females. For *S. crassipes*, the greater activity of the males is partially attributed to their frequent foreleg Tapping (Aspey, 1974), since females do not exhibit such behavior. Whereas most females remained motionless throughout the observation period, males were rarely stationary.

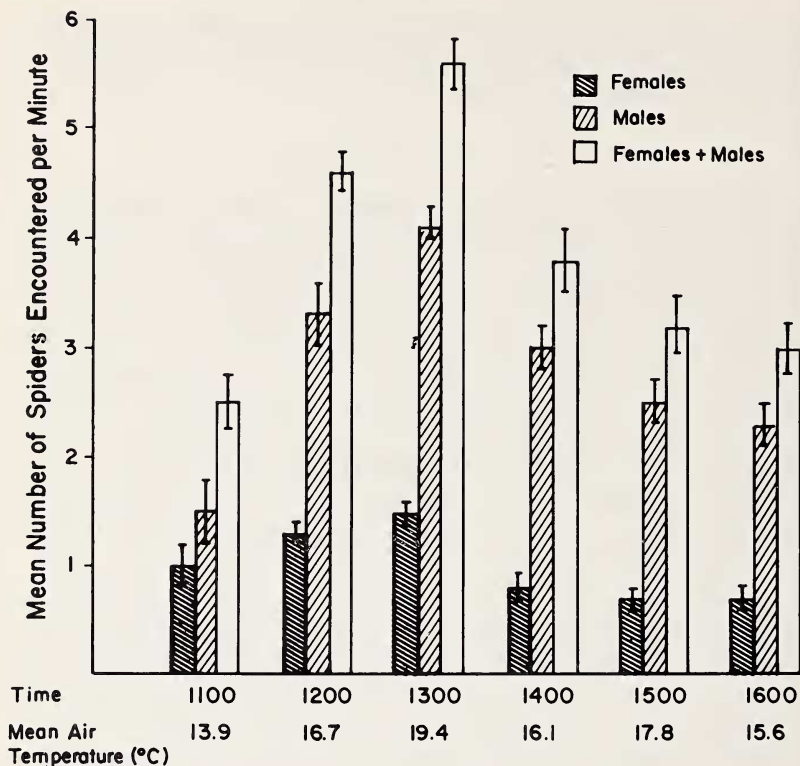


Fig. 1. The mean number of individual conspecifics crossing within 1 cm in front of adult male *Schizocosa crassipes* in the natural habitat on 7 days during May 19-31, 1973, from 1100-1600 hours. Each "Females + Males" histogram bar at each hour interval represents the mean number of spiders observed during 175 one-minute observation periods.

These differences in motility were consistent with the sexually dimorphic coloration and patterning in *S. crassipes*. To illustrate, the relatively stationary mottled brown female camouflages well with the surrounding leaf litter. In contrast, the males stand out prominently in the natural habitat, actively announcing their presence to conspecifics using a variety of visual (Aspey, 1976a, b) and acoustic (Rovner, 1975) signals. Apparently, fewer natural pressures have existed favoring camouflage for the males since their activity would have revealed their location regardless of pro-

tective coloration. In fact, selection pressures in *S. crassipes* have obviously favored conspicuous males given their extensive behavioral repertoire during male-male and male-female interactions.

Of the ecological and behavioral factors previously mentioned that possibly determine the edge effect, food availability in *S. crassipes* seems the least prominent. Although Luczak and her colleagues attributed high concentrations of lycosids at the forest-meadow interface to large populations of mosquitos, other investigators (Clark and Grant, 1968; Dabrowska-Prot and Luczak, 1968) showed that the introduction of wandering spiders above normal densities in field enclosures resulted in increased cannibalism among the spiders without proportionately greater effects on the prey species. Although a food-dependent factor may operate in making *S. crassipes* an edge species, high concentrations of prey species were not obvious in the study area, and the elaborate behavioral displays of the males appear to minimize intraspecific cannibalism. Instead, field observations suggest that microclimate is a controlling factor in determining high densities of spiders.

The natural edge habitat where *S. crassipes* was found in abundance could be divided into sunny and shaded portions. Although the spiders were restricted to a margin approximately 2 m wide, predictions as to whether they would be found in the sunny or shaded area could be made by knowing the previous day's rainfall and temperature. When temperature was high and rainfall infrequent, the spiders were found almost exclusively in the shaded area. This area provided for regulation of temperature during prolonged heat spells, as well as for sources of moisture trapped under leaf litter. Spiders were found in the sunny region following a day of rain or when temperatures were cooler. It appears, therefore, that *S. crassipes* relocate in their microenvironment according to weather conditions.

Finally, with regard to social behavior, laboratory observations of grouped *S. crassipes* have indicated that some form of social attraction exists. In groups of five spiders, three or four spiders at any point in time aggregate, maintaining inter-individual distances of 3-5 cm (Aspey, 1976b). Similarly, in the field *Pardosa* spp. have been observed to maintain a "mobile territory" (i.e., inter-individual distance) of approximately 7.5 cm in diameter (Dr. B. Vogel, personal communication). Although the basis for this aggregation is unknown, silk draglines may provide the stimu-

lus that keeps the spiders together, since Dijkstra (1975) found that both male and female *P. amentata* prefer areas where draglines of both sexes have been laid. This preference for areas having silk of both sexes present may explain why females remain in the aggregation. Males remain in such areas due to a sex pheromone(s) presumably contained in (on) the female's silk (Kaston, 1936; Hedgekar and Dondale, 1969; Richter, Stolting, and Vlijm, 1971). Furthermore, frequent displays and interactions by males would contribute to reduce locomotion into surrounding areas. On one hand, *S. crassipes* are attracted to one another and frequently interact, encountering an average of four conspecifics per minute. On the other hand, displays occurring during male-male agonistic interactions may serve to space individuals so that no spider intrudes on the personal space of another (Aspey, 1976b).

The edge effect in *S. crassipes* appears influenced by complex interactions among ecological and behavioral variables. Although food availability and environmental conditions may initially attract spiders to an edge habitat, predictions concerning the location of large spider populations within the habitat seem more influenced by microclimatic variables. Furthermore, social attraction among conspecifics maintain an aggregation within the restricted region. Thus, a delicate balance of social attraction modulated by definite inter-individual spacing interacts with ecological variables to produce the phenomenon of the edge effect in *S. crassipes*.

ACKNOWLEDGMENTS

I gratefully acknowledge Dr. Jerome S. Rovner, Department of Zoology and Microbiology, Ohio University, for his helpful guidance and encouragement throughout this research, and for his useful discussions of the material. Drs. S. W. F. van der Ploeg and H. Dijkstra, Free University, Amsterdam, The Netherlands, kindly offered helpful discussions and commented on the material.

LITERATURE CITED

ALMQUIST, S.

1973. Habitat selection by spiders on coastal sand dunes in Scania, Sweden. *Entomol. Scand.* 4: 134-154.

ASPEY, W. P.

1974. Wolf spider sociobiology: An ethological and informational theory analysis of agonistic behavior in *Schizocosa crassipes*. Doctoral Dissertation, Ohio University, Athens, Ohio 45701.

1975. Ontogeny of display in immature *Schizocosa crassipes* (Araneae: Lycosidae). *Psyche*. **82**: 174-180.
- 1976a. Wolf spider sociobiology: I. Agonistic display and dominance-subordination relations in adult male *Schizocosa crassipes*. *Behaviour* (in press).
- 1976b. Wolf spider sociobiology: II. Density parameters influencing agonistic behavior in *Schizocosa crassipes*. *Behaviour* (in press).
- ASPEY, W. P., C. M. LENT, AND M. A. MEEKER
1972. Effect of humidity and desiccation by living and dead wolf spiders (Araneae: Lycosidae). *Experientia*. **28**: 1249-1250.
- BEECHER, W. J.
1942. *Nesting Birds and the Vegetation Substrate*. Chicago: Chicago Ornithological Society.
- CLARK, R. D. AND P. R. GRANT
1968. An experimental study of the role of spiders as predators in a forest litter community. Part 1. *Ecology*. **49**: 1152-1154.
- DABROWSKA-PROT, E. AND J. LUCZAK
1968. Spiders and mosquitos of the ecotone of alder forest (*Carici elongatae-alnetum*) and oak-pine forest (*Pino-Quercetum*). *Ekol. Pol., Ser. A*. **16**: 461-483.
- DABROWSKA-PROT, E., J. LUCZAK, AND K. TARWID
1966. Experimental studies on the reduction of the abundance of mosquitos by spiders. KKK. Indices of prey reduction and some controlling factors. *Bull. Acad. Pol. Sci.* **14**: 777-782.
- DIJKSTRA, H.
1975. Meeting of the sexes in *Pardosa amentata* (Clerck) (Araneae, Lycosidae). *Proc. Sixth Int. Cong. Arach., Amsterdam, 1974*. **VI**: 125.
- EDGAR, W. D.
1971. The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa (Pardosa) lugubris*, in central Scotland. *J. Anim. Ecol.* **40**: 303-322.
- FITCH, H. S.
1963. Spiders of the University of Kansas Natural History Reservation and the Rockefeller Experimental Tract. *Misc. Publ., Mus. Nat. Hist., Univ. Kansas*. **33**: 1-202.
- GILLETT, S.
1968. Airborne factor affecting the grouping behaviour of locusts. *Nature*. **218**: 782-783.
1972. Social aggregation of adult *Schistocerca gregaria* and *Locusta migratoria migratoriodes* in relation to the final moult and ageing. *Anim. Behav.* **20**: 526-533.
1973. Social determinants of aggregation behaviour in adults of the desert locust. *Anim. Behav.* **21**: 599-606.
- HALLANDER, H.
1967. Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O. F. Müller). *Oikos*. **18**: 145-150.
- HEDGEKAR, B. M. AND C. D. DONDALE
1969. A contact sex pheromone and some response parameters in lycosid spiders. *Can. J. Zool.* **47**: 1-4.

- JOHNSON, D. W. AND E. P. ODUM
 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology*. **37**: 50-62.
- KASTON, B. J.
 1936. The senses involved in the courtship of some vagabond spiders. *Entomol. Am.* **16**: 97-167.
- KUENZLER, E. J.
 1958. Niche relations of three species of lycosid spiders. *Ecology*. **39**: 494-500.
- KULLMANN, V. E.
 1968. Soziale phenomene bei spinnen. *Insectes Sociaux*. **15**: 289-298.
- LUCZAK, J.
 1966. The distribution of wandering spiders in different layers of the environment as a result of interspecies competition. *Ekol. Pol., Ser. A*. **14**: 233-244.
- LUCZAK, J. AND E. DABROWSKA-PROT
 1966. Experimental studies on the reduction of the abundance of mosquitos by spiders. I. Intensity of spider predation on mosquitos. *Bull. Acad. Pol. Sci. cl. II*. **14**: 315-320.
- NØRGAARD, E.
 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. *Oikos*. **3**: 1-21.
- ODUM, E. P.
 1959. *Fundamentals of Ecology*. Philadelphia: W. B. Saunders Company.
- RICHTER, C. J. J., J. DEN HOLLANDER, AND L. VLIJM
 1971. Differences in breeding and motility between *Pardosa pullata* (Clerck) and *Pardosa prativaga* (L. Koch), (Lycosidae, Araneae) in relation to habitat. *Oecologia*. **6**: 318-327.
- RICHTER, C. J. J., H. C. J. STOLTING, AND L. VLIJM
 1971. Silk production in adult females of the wolf spider *Pardosa amentata* (Lycosidae, Araneae). *J. Zool. Lond.* **165**: 285-290.
- ROVNER, J. S.
 1975. Sound production by Nearctic wolf spiders: A substratum-coupled stridulatory mechanism. *Science*. **190**: 1309-1310.
- SHEAR, W. A.
 1970. The evolution of social phenomena in spiders. *Bull. Brit. Arach. Soc.* **1**: 65-76.
- SIEGEL, S.
 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill Book Company.
- VLIJM, L., J. DEN HOLLANDER, AND S. E. WENDELAAR BONGA
 1970. Locomotory activity and sexual display in *Pardosa amentata* (Cl.) (Lycosidae, Araneae). *Neth. J. Zool.* **20**: 475-484.
- WILSON, E. O.
 1971. *The Insect Societies*. Cambridge: The Belknap Press of Harvard University.